

A phylogenetic analysis of the southern pines (*Pinus* subsect. *Australes* Loudon): biogeographical and ecological implications

Dean C. Adams and James F. Jackson

(DCA) Department of Ecology and Evolution, State University of New York at Stony Brook,
Stony Brook, New York 11794-5245, U.S.A.;

(JFJ) Department of Biology, University of Southwestern Louisiana, Lafayette,
Louisiana 70504, U.S.A.

Abstract.—A parsimony analysis on morphological characters was performed to estimate the phylogenetic relationships of the taxa of *Pinus* subsect. *Australes*. The Adams consensus tree placed the Caribbean species as a monophyletic clade with *P. rigida*–*P. serotina* as its sister taxon. Based on this phylogeny, area cladograms were constructed and compared to geologic cladograms constructed from plate-tectonic evidence. This comparison and an ancestral area analysis indicate that colonization of the tropics most likely occurred from Florida to Hispaniola, rather than by the circumferential-Gulf route. Subsequent dispersal events to Central America, Cuba, and the Bahamas are proposed to explain the geographic distribution of *P. caribaea*. Ecological comparisons within subsect. *Australes* found that sister species are not syntopic and that syntopic species are not sister species. Although some North American sister species are ecologically quite different, there is low ecological diversity among the Caribbean species.

Pinus is one of the most widespread genera of plants in the northern hemisphere (Mirov 1967:307–308; Strauss & Doerksen 1990). Its species are found from Central America and Sumatra to the Arctic circle (Little & Critchfield 1969, Strauss & Doerksen 1990, Farjon 1996), occupy xeric to mesic habitats, and comprise one of the dominant vegetation types on the earth. They are important economically, being used for fuel and lumber, and are frequently planted for commercial purposes in parts of the world where they do not naturally occur (Mirov 1967:451). While often considered early successional species well-adapted to poor soils (Govindaraju 1984), pines are actually ecologically diverse and are found from sea level to the timberline, from seasonally wet savannas to deserts, and from monotypic stands to multispecies climax forests where there is co-occurrence with

hardwoods. McCune (1988) characterized the ecological diversity for North American pines and defined five ecological groups: (1) fire-resistant species, (2) mesophytic shade-tolerant species, (3) stress-tolerant species, (4) fire-resilient species, and (5) southern mesic species.

Other studies provide a more quantitative assessment of the interaction between pines and their environment. In particular, studies of bark ontogeny and fire have shown most pines to be particularly well adapted to surviving surface fires (Harmon 1984, D. C. Adams 1994). Recent work by Jackson and Adams demonstrates the evolution of negative bark allometry (D. C. Adams & Jackson 1995) in species whose habitats are characterized by frequent surface fires. This finding is consistent with models of defensive structure evolution, where resources are allocated

earlier to defense as the likelihood of a mortality factor increases.

Although the ecological roles of pines are relatively well defined, aspects of the classification and systematics of the genus *Pinus* have been uncertain (Mirov 1967: 540, Strauss & Doerksen 1990). Shaw (1914) published the first major taxonomic work on pines, where he recognized two subgenera, *Strobus* and *Pinus*. Pilger (1926) presented a second classification of the pines, classifying many of Shaw's (1914) varieties as species and further dividing the subgenera into eleven sections. Because of his heavy reliance on needle number, however, Pilger's classification is considered to be a step backwards (Mirov 1967:526). Duffield (1952) revised the classification of the pines, using information from hybridization studies. He divided Shaw's "Group *Australes*" into two "Groups," the eastern species (XI) and the western species (XII). In Shaw's (1914) classification, most of the southern pines (*P. echinata*, *P. elliottii*, *P. glabra*, *P. palustris*, and *P. taeda*) as well as the Caribbean and many western species, were included in the "Group *Australes*". Duffield also added three species from Shaw's "Group *Insignes*" to his "Group XI": *P. rigida*, *P. serotina*, and *P. pungens*. Little & Critchfield (1969) reviewed the many classification schemes for *Pinus*. In particular, they restored the name *Australes*, at the subsectional rank, to Duffield's "Group XI," which now included the eight southern pines and three Caribbean species.

With the advent of phylogenetic methodology, many subsections of the genus *Pinus* have been reexamined in an evolutionary context, so that the relationships among many of the North American taxa are now better known (Wheeler et al. 1983, Strauss & Doerksen 1990, Malusa 1992, Govindaraju et al. 1992, Krupkin et al. 1996). The species comprising subsect. *Australes*, however, have not been examined in a phylogenetic context. In particular, it is of interest to determine whether the Caribbean taxa comprise a monophyletic clade and, if so,

what its relationship is to the North American species. Mirov (1967:555) thought that insular varieties of *P. caribaea* originated from a Central American progenitor, but without a phylogenetic analysis he could not specify whether this was the original colonization of the Caribbean islands by subsect. *Australes* or was part of a subsequent radiation within the Caribbean region. Farjon (1996) on the other hand, suggested that the Caribbean taxa were of a North American origin, and that the Central American *P. caribaea* originated from Caribbean immigrants. Because of these outstanding questions, we felt that an examination of the relationships of the taxa in subsect. *Australes* was needed, and therefore performed a phylogenetic analysis of the southern pines using morphological characters. In addition, we generated an area cladogram for the geographic regions occupied by the taxa and compared this to geologic evidence in order to better understand the vicariance and dispersal of the taxa in the Caribbean.

Methods

Phylogenetic analysis.—The eight species of subsect. *Australes* in the eastern United States and certain geographically defined OTUs of the three Caribbean species were used in this study (Appendix I). *Pinus caribaea* from the Bahamas, Cuba, Belize, and Honduras-Nicaragua were treated as separate OTUs. Because *P. caribaea* in the uplands of Belize and Honduras may be subject to hybridization with *P. oocarpa* (Williams 1955) we used only specimens from lowland localities. *Pinus elliottii* var. *densa* was also treated as a separate OTU. The subsection *Australes* is included within the hard pines (subg. *Pinus*) as classified by Little & Critchfield (1969). While the relationships among the hard pines are still somewhat controversial (see Strauss & Doerksen 1990, Govindaraju et al. 1992), we chose to use two taxa (*P. virginiana* and *P. clausa*) from subsect. *Contortae* as out-

Table 1.—Data matrix for the taxa of *Pinus* used in this study. Descriptions of characters and character codes are found in Appendix II.

Species	Character states
<i>P. caribaea</i> —Bahamas	0000101011 1101311112 7
<i>P. caribaea</i> —Belize	0001111011 1101411111 8
<i>P. caribaea</i> —Cuba	0000111001 1100511111 9
<i>P. caribaea</i> —Honduras—Nicaragua	0001111011 1101411112 6
<i>P. clausa</i>	0010101110 3100100000 2
<i>P. cubensis</i>	0000111011 1111211014 7
<i>P. echinata</i>	0000011111 1100200000 2
<i>P. elliottii</i> var. <i>elliottii</i>	1000110011 1100211012 2
<i>P. elliottii</i> var. <i>densa</i>	1000111011 1100211013 3
<i>P. glabra</i>	0000011111 1100100000 2
<i>P. occidentalis</i>	0000101011 1101611113 3
<i>P. palustris</i>	1001100000 2000401113 0
<i>P. pungens</i>	1101100000 3100201005 0
<i>P. rigida</i>	0000111011 3100411102 1
<i>P. serotina</i>	0000111011 2101511102 0
<i>P. taeda</i>	1101100000 3100301100 4
<i>P. virginiana</i>	0010101110 3100101000 5

groups, based on the phylogenies of Govindaraju et al. (1992) and Farjon (1996).

Twenty one morphological characters were scored from herbarium specimens (LAF, MO, NY), with supplementary information from North American specimens collected by us and from literature sources (Farjon & Styles 1997, Radford et al. 1964); species were assigned values based on an average of several specimens. Fourteen characters were based on cone morphology and seven on needle morphology (Appendix II). Four of these characters were coded as ordered, multi-state characters (Table 1; Appendix II). Binary scoring was employed for the remainder. While recognizing that some of the characters are quantitative (Stevens 1996), we believe binary scoring adequately approximates character states among taxa where we have used it. We generated a phylogenetic hypothesis through Wagner parsimony using the branch and bound algorithm in PAUP version 3.1 (Swofford 1991). Wagner parsimony attempts to reconstruct an evolutionary tree by minimizing the number of changes of the character states along the

tree (Kluge & Farris 1969, Strauss & Doerksen 1990). If one assumes that a species from a closely related group reflects previous character states, it can be used as an outgroup to root the tree and to polarize the character states as well (Wiley 1981).

Biogeographic analysis.—Comparing the current distributions of taxa with their phylogenetic history to elucidate patterns, as well as to evaluate the relative plausibilities of vicariance and dispersal, is the purpose of cladistic biogeography (Nelson & Platnick 1981, Wiley 1988, Morrone & Crisci 1995). To examine the biogeography of subsect. *Australes* in a phylogenetic context, we used the method outlined by Brooks & McLennan (1991). After the phylogenetic relationships were estimated, the geographic areas containing the taxa were defined: eastern North America (NA), the Bahamas (B), Cuba (Cb), Hispaniola (H), the Yucatan peninsula (Y), and Honduras-Nicaragua (Ch). The relationships of these geographic areas were then determined by representing the relationships of the taxa by a matrix containing additive binary codes, replacing the species with their respective geographic areas, and performing a parsimony analysis. Brooks Parsimony Analysis (BPA) has been criticized for its treatment of widespread taxa as synapomorphic for areas (Kluge 1988) and as a method for generating general area cladograms (Nelson & Ladiges 1991). Our goal was to evaluate alternative historical biogeographies rather than to produce a general area cladogram. Having treated the species population of each major Caribbean locale as an OTU, our data set did not, by definition, have widespread taxa, but there was a redundant distribution with two OTUs in Cuba. We chose to derive area cladograms by BPA with (inclusive ORing: Cressey et al. 1983) and without redundant distributions in order to evaluate the redundancy (Brooks 1990). The ancestral area of the Caribbean taxa was estimated by the technique of Bremer (1992). This involves comparing areas in regard to the numbers of necessary gains

and losses in the area cladogram by Camin-Sokal parsimony and under the assumption that each area is ancestral. The putative ancestral area best supported by the biogeographic evidence is that having the highest ratio of gains to losses.

Phylogenetically-based cladograms are intended for comparison with geological area cladograms. Much work has been done on the biogeography of the Caribbean flora and fauna (e.g., Rosen 1976, 1978, 1985; Guyer & Savage 1986; Page & Lydeard 1994; Hedges et al. 1994). However, due to the complex geologic history of the region (see Pindell & Barrett 1990), many of the interpretations of biogeography are highly controversial and out of date. In light of the increased knowledge of Caribbean geology (Burke 1988, Pindell & Barrett 1990), we felt that using geologic cladograms from previous biogeographic work might be unwise. We therefore compared the area cladograms for subsect. *Australes* to geologic cladograms generated from recent tectonic evidence on the relationships of the geologic regions of the Caribbean.

Results

Phylogenetic analysis.—We found three most parsimonious trees from our cladistic analysis, each containing 81 steps and a consistency index (CI) of 0.469 (Fig. 1). When uninformative characters were excluded, the consistency index was reduced by only 0.010 to CI = 0.459, implying that most characters were phylogenetically informative. From these three most parsimonious trees we generated a consensus tree, using the procedure described by E. N. Adams (1972, 1986). This tree contains only that information present in all rival tree topologies, and is thus a conservative estimate of the true topology.

Based on this phylogeny, subsect. *Australes* is divided into several distinct subclades. The smaller subclade is a polytomy containing *P. taeda*, *P. pungens*, and *P. palustris*. A second polytomy is located deep-

er in the phylogeny and contains the smaller subclade, the larger subclade, and *P. echinata* and *P. glabra* as single taxa. The remaining taxa are all found within the larger subclade. That the phylogeny locates *P. rigida* and *P. serotina* as sister taxa accords with the proposal by Smouse and Saylor (1973), who consider them conspecific. The most significant aspect of this phylogeny is that the Caribbean species are monophyletic within the larger subclade.

Within the larger subclade, it is noteworthy that *P. elliotii* var. *densa* is the sister taxon to *P. elliotii* var. *elliotii*. Based on the chemical composition of its turpentine, Mirov et al. (1965) and Mirov (1967:555) proposed that *P. elliotii* var. *densa* was more closely related to the Caribbean species, and was a recent arrival to Florida. Our findings suggest that it is in fact more closely related to the mainland slash pine than to any Caribbean taxon. In addition, our phylogeny suggests that *P. cubensis* is more closely related to *P. caribaea* than to *P. occidentalis*, in contradiction to the proposal by Mirov (1967:232). Our findings place *P. occidentalis* basal to the Caribbean subclade.

Biogeographic analysis.—Much of the history of the Caribbean region is still unknown, as is evident from the numerous tectonic models of the region (Perfit & Williams 1989). However, the present study focuses on taxa in the Greater Antilles, the Bahamas, the Yucatan peninsula, and Honduras-Nicaragua, where there seems to be a general consensus of opinion concerning the geologic history. We therefore present a brief account of the geologic history of the region (summarized in Fig. 2) and use this to generate geologic cladograms for the taxa.

Mexico collided with the North American plate during the Jurassic (Burke 1988, Pindell & Barrett 1990). The Greater Antilles were part of a larger body called the Great Arc, which originated in the Pacific during the late Cretaceous and migrated northeast into the Atlantic in the Paleocene

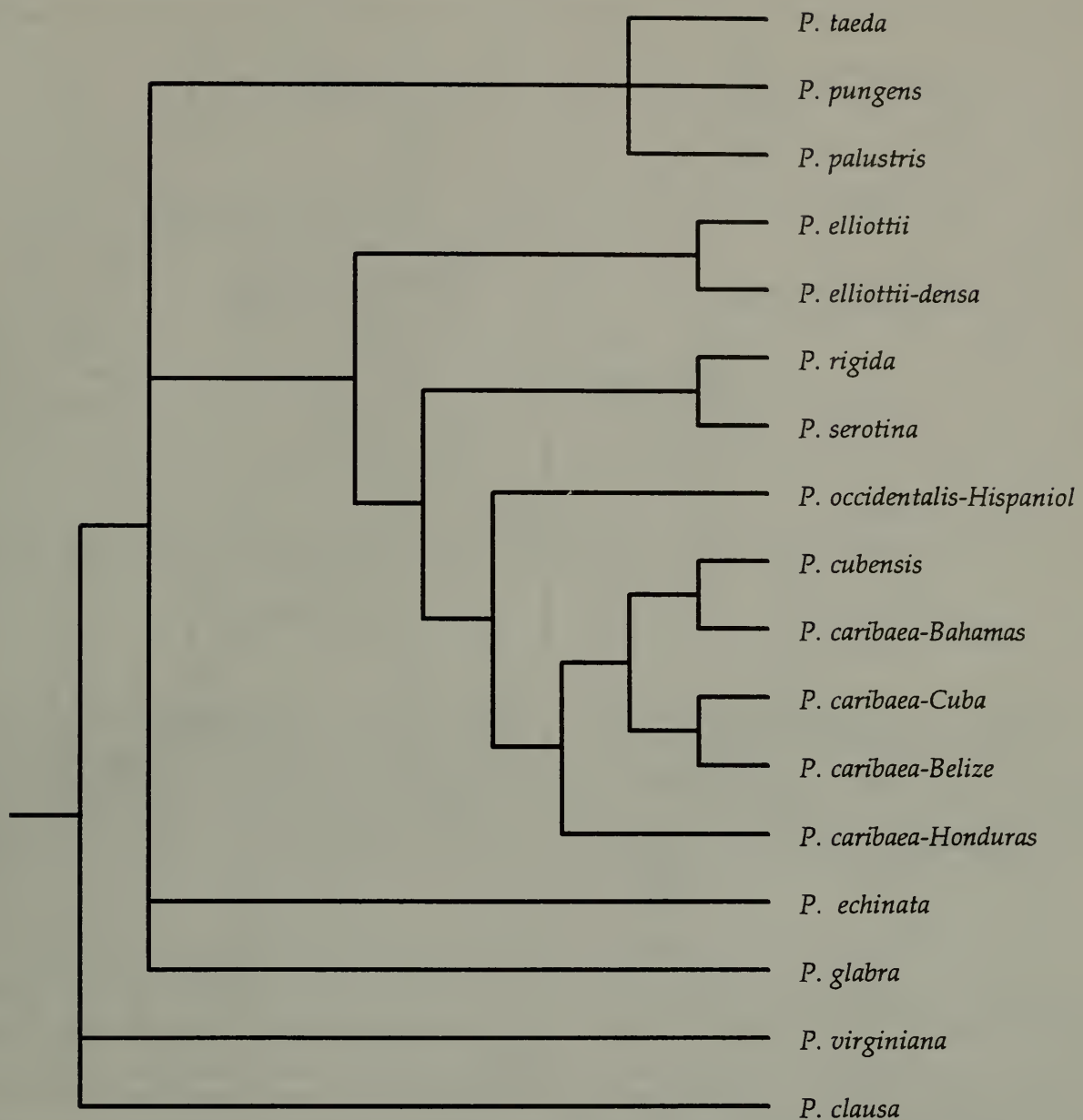


Fig. 1. Adams consensus tree found from three most parsimonious trees based on twenty-one morphological characters of *Pinus* spp.

(Burke 1988, Pindell & Barrett 1990). The Great Arc broke into three segments sometime in the late Cretaceous to early Paleocene (Burke 1988). The northern segment became the Greater Antilles, the central became the Lesser Antilles, and the southern segment is presumed to have collided with the South American continent.

During the late Paleocene, the Greater Antilles began to collide with the Bahaman plate (Pindell & Dewey 1982, Burke 1988, Pindell & Barrett 1990). However, Burke (1988) claims that prior to this, the Greater Antilles collided with the Yucatan. Others

(Pindell & Barrett 1990) claim that although there is geologic evidence for such a collision, it cannot be determined whether it was the Greater Antilles or some other geologic body that collided with the Yucatan. Strike-slip faults began to separate Cuba and Hispaniola in the mid-Eocene (Pindell & Barrett 1990), and the Honduras-Nicaraguan block (called Chortis) began to collide with the Yucatan shortly after in the Miocene (Perfit & Williams 1989). Though Pindell and Barrett place this collision slightly earlier in the Oligocene, this does not affect our geologic cladograms. Based



Fig. 2. Tertiary paleogeography of the Caribbean (redrawn from Perfit and Williams 1989). A. Late Cretaceous. B. Paleocene. C. Mid-Eocene. D. Late Miocene-Pliocene. AR = Aves Ridge, B = Bahaman Platform, CA = Cuban Arc, CH = Chortis, H = Hispaniola, J = Jamaica, L = Lesser Antilles Arc, NH = North Island of Hispaniola, SH = South Island of Hispaniola.

on this geologic information, we have constructed two area cladograms (Figs. 3a, b). The first (Fig. 3a) represents the relationships of the areas if the Yucatan had not collided with the Greater Antilles (*sensu* Pindell & Barrett 1990), and the second (Fig. 3b) if it had (*sensu* Burke 1988).

The taxon-based area cladogram derived with inclusive ORing has Hispaniola as the sister area to the other Caribbean areas and situates Cuba as the sister area to the Yucatan, in a derived position (Fig. 4a). The taxon-based area cladogram that treated

Cuba as two separate areas historically (exclusive ORing) has a pattern of branching identical to that of the taxon cladogram, but with Cuba as a sister area to both the Yucatan and the Bahamas (Fig. 4b). The ancestral area analysis (AAA) of Bremer (1992) was carried out in two ways: on an area cladogram with terminal sister taxa not grouped, which corresponds to Fig. 4b; and on an area cladogram that considered there to be no node separating the two OTUs of *P. caribaea* of Cuba and Belize. The logic of combining the areas of the terminal sister

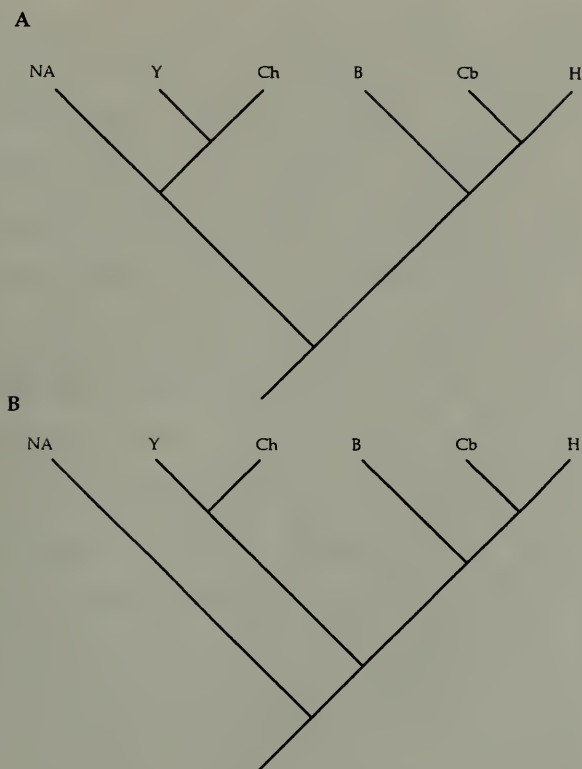


Fig. 3. Geologic cladograms based on tectonic evolution in the Caribbean. (A) corresponds to hypothesis of Pindell and Barrett (1990), where the Yucatan did not collide with the Greater Antilles; (B) corresponds to Burke's (1988) hypothesis, which includes this collision.

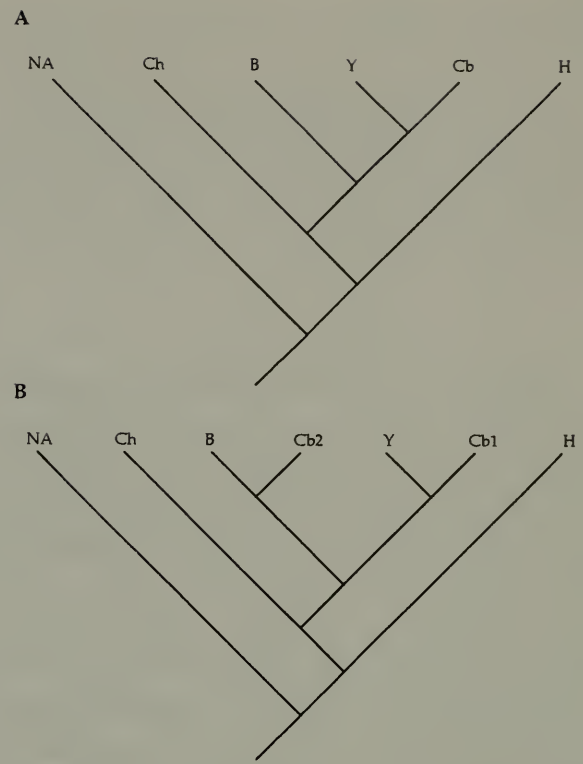


Fig. 4. Area cladograms of six geographic localities based on the phylogeny for *Pinus* subsect. *Australes* using: (A) inclusive ORing, and (B) exclusive ORing. Letters correspond to the different geographic regions: NA = southern United States, Ch = Chortis, B = Bahamas, Y = Yucatan, Cb = Cuba, H = Hispaniola.

taxa from this node is that the taxa are conspecific. For both approaches to AAA, Hispaniola is the most probable ancestral area, and Cuba is the next most probable (Table 2).

The positions of Yucatan-Chortis and Hispaniola differ between the geological and taxon-based area cladograms (Figs. 3 and 4). In the geological area cladograms, Yucatan-Chortis is either the sister area to North America or the basal area in the Caribbean, whereas the taxon-based area cladograms have Yucatan-Chortis separated and both in more derived positions. Hispaniola is placed near the origin of the Caribbean subclade by the taxon-based area cladogram, but in a derived position by the geological data. We conclude that the cladogram based on geological contact and separation corresponds poorly to the sequence of areas colonized by the Caribbean taxa of subsect. *Australes*.

The derived placement of Cuba in the

taxon-based area cladogram calculated by inclusive ORing is due to there being two derived taxa (*P. cubensis* and *P. caribaea*) on Cuba that determine the location of Cuba on the area cladogram (Brooks &

Table 2.—Estimation of ancestral area for the Caribbean subclade of the subsection *Australes*. Values not in parentheses are for cladogram that reduces conspecific sister taxa. Values in parentheses are for cladogram without reduction of conspecific sister taxa. G = number of necessary gains under forward Camin-Sokal parsimony. L = number of necessary losses under reverse Camin-Sokal parsimony. AA = G/L rescaled by division by the largest G/L. \overline{AA} = mean of AA's calculated by the two reduction alternatives.

Area	G	L	G/L	AA	\overline{AA}
Hispaniola	1 (1)	1 (1)	1.00 (1.00)	1.00 (1.00)	1.00
Cuba	2 (2)	3 (4)	0.67 (0.50)	0.67 (0.50)	0.59
Chortis	1 (1)	2 (2)	0.50 (0.50)	0.50 (0.50)	0.50
Yucatan	1 (1)	3 (4)	0.33 (0.25)	0.33 (0.25)	0.29
Bahamas	1 (1)	4 (4)	0.25 (0.25)	0.25 (0.25)	0.25

McLennan 1991:212). The presence of derived taxa and the lack of ancestral taxa on Cuba can be explained through intra-Cuban differentiation combined with colonization of other Caribbean areas from Cuba. The AAA clearly supports this explanation.

Discussion

Based on our phylogenetic hypothesis of the southern pines, several ecoevolutionary trends can be recognized. First, sister species are not syntopic. For example, the sister clades of *P. rigida* and *P. serotina* as well as *P. cubensis* and *P. caribaea* represent taxa that are allopatric. *Pinus pungens* and *P. palustris* are allopatric as well and occupy different habitats. Second, species that are syntopic are not sister species. Examples of this are *P. palustris* and *P. elliottii* in the eastern Gulf coastal plain flatwoods, *P. palustris* and *P. echinata* in the uplands of the western Gulf coastal plain, and *P. taeda* and *P. echinata* in the southern Piedmont.

Major ecological divergence is found between some sister species. For example, *P. pungens* grows in dense monospecific stands in xeric montane locations and maintains dominance by mass recruitment after stand-replacing crown fires; its bark grows with positive allometry (Adams 1994). In comparison, *P. palustris* grows as widely spaced individuals in parkland vegetation subject to frequent surface fires, and early life history stages of this species are fire-resistant (McCune 1988), as typified by its "grass" stage and negative allometry of bark. Curiously, there is a general lack of ecological divergence in the Caribbean subclade of subsect. *Australes* (Smith 1954). This subclade is less diverse in that there are no mountain ridge specialists like *P. pungens*, there are no shade-tolerant species like *P. glabra*, and there are no species with a fire-resistant seedling stage like *P. palustris* or *P. elliottii* var. *densa*.

The purpose of cladistic biogeography is to attempt to discern whether current dis-

tribution patterns are the result of vicariance or dispersal. In subsect. *Australes* this issue is related to whether the initial colonization of Caribbean islands was from eastern North America or from Central America. Both the ancestral area analysis and the fact that neither Yucatan nor Chortis branch low on the area cladogram suggest that the Greater Antilles were the first sites of colonization in the Caribbean. This could have occurred by dispersal from North America in the late-Tertiary or Quaternary, or by vicariance from Central America if a component of Hispaniola collided with, and then separated from, Yucatan during the Paleocene (Burke 1988). The issue is one of timing and therefore cannot be decided conclusively without molecular data on the divergence time between North American and Caribbean taxa. However, several facts argue in favor of dispersal to Hispaniola. For example, there is no evidence in Central America of a Caribbean ancestor; *P. caribaea* cannot play this role given its derived status. The Caribbean subclade was derived from an ancestor that shared many traits, particularly of cones, with *P. serotina*. Currently *P. serotina* has an Atlantic-East Gulf Coastal Plain distribution, not being found west of Mobile Bay. This puts *P. serotina* geographically closer to the late-Tertiary Greater Antilles than to the putative contact between the Yucatan and the proto-Greater Antilles. In addition, the lack of ecological diversification in the Caribbean clade could suggest an occupation of the region too recent to have occurred via Paleocene vicariance. Farjon (1996) found that *P. occidentalis* and *P. caribaea* var. *hondurensis* formed a sister group to all the other neotropical pines he considered, a result consistent with derivation from a southeastern North American ancestor.

Dispersal of *Australes* to the Greater Antilles may have been part of a pattern of colonization by xeric-adapted biota. R. P. Adams (1989) presented evidence from leaf morphology and volatile leaf oils that strongly indicates an origin of West Indian

Juniperus species from eastern North America, rather than from Mexico. Buck (1990) suggested that several xeric bryophyte species found in North America and upland Hispaniola colonized the island via dispersal during glacial episodes of the Pleistocene when over-water distances were less due to lower sea levels (Gascoyne et al. 1979) and when savanna habitats were more widespread than at present because of a more xeric climate (Pregill & Olson 1981). Such a scenario could apply to colonization of the Greater Antilles by subsect. *Australes* as well as to inter-island movement and colonization of Central America.

Mirov (1967:555) hypothesized that *P. caribaea* colonized the Caribbean islands from Central America. The area cladogram, with Chortis as the sister area to all other areas occupied by *P. caribaea*, supports this direction of colonization in the species. Dispersal is implicated because no connection is known to have existed between Chortis and the Greater Antilles. The only possibility of vicariance within the *P. caribaea* clade would be between the taxonomic subunits in Cuba and Yucatan. However, any such vicariance would date from early Tertiary (Burke 1988), and this appears too longstanding for the small level of differentiation between the taxa. It is difficult to ascribe any of the divergences within the Caribbean subclade to vicariance.

It was believed by Mirov et al. (1965) that *P. elliotii* var. *densa* was a recent immigrant to Florida from the Caribbean and that it was therefore more closely related to the Caribbean species. Our results place *P. elliotii* var. *densa* as the sister taxon to *P. elliotii* var. *elliotii*, suggesting that it is more closely related to the mainland species. Squillace (1966) demonstrated multi-character clinal variation between *P. elliotii* var. *elliotii* and *P. elliotii* var. *densa* in central Florida. We also found that *P. cubensis* is more closely related to *P. caribaea* than to *P. occidentalis*. Mirov (1967:232) had proposed that *P. cubensis* and *P. occidentalis* were closely related taxa. Clearly

more work is needed to determine their relationship.

Klaus (1980) suggested that, for comparisons through nodes deep within the phylogeny of *Pinus*, cones display primitive character states at the apex and derived states at the base. Consideration of intra-cone character variation in the context of the subject. *Australes* cladogram provides evidence of this phenomenon at a finer phylogenetic scale. *Pinus glabra*, *P. elliotii*, and *P. rigida* often have flattened, distally-pointed umbos at the cone base and more erect umbos at the apex. Within the cladogram, erect umbos characterize the outgroup and the *P. taeda*-*P. pungens*-*P. palustris* subclade, whereas flattened umbos are typical in *P. serotina* and the Caribbean subclade. In *P. caribaea* var. *hondurensis*, the umbo spine tends to be unconnected to the keel on basal scales, a character state more widespread in *P. cubensis* cones, but connected to the keel on apical scales, a state found throughout the cone in taxa derived from nodes below *P. caribaea* var. *hondurensis*. A counterexample, however, exists in the relatively erect umbos apically in some *P. caribaea* var. *hondurensis*. This character state is derived if the Caribbean clade arose through an ancestor like *P. occidentalis*, yet it appears at the apex.

Our phylogenetic hypothesis of subsect. *Australes* is a first step in understanding the history of the pines of the southern United States and the Caribbean. Based on this phylogeny, we have identified possible dispersal and vicariance events and have provided a framework on which future studies may be based. While it is appealing to interpret phylogenetic hypotheses as reconstructions of evolutionary history, it must be stressed that they are only estimations of the true topology based on the available data. Studies have shown that most phylogenetic methods can perform rather poorly in their estimation of true tree topology (Fiala & Sokal 1985; Rohlf et al. 1990). We therefore present this phylogenetic hypoth-

esis as a tentative estimation of the relationships of the southern pines.

Acknowledgments

We thank the Herbaria of the New York and Missouri Botanical Gardens and the University of Southwestern Louisiana for providing specimens. We thank A. Farjon for comments on an earlier version of the manuscript, Ursula Jackson for drawing Fig. 2, and W. D. Reese for taxonomic counsel. This work is contribution number 998 from the program in Ecology and Evolution at the State University of New York at Stony Brook.

Literature Cited

- Adams, D. C. 1994. Defensive structures in the genus *Pinus*: heterochronic changes in bark ontogeny. Unpublished M.S. Thesis, University of Southwestern Louisiana, Lafayette, 83 pp.
- , & J. F. Jackson. 1995. Estimating the allometry of tree bark.—*American Midland Naturalist* 134:99–106.
- Adams, E. N. III. 1972. Consensus techniques and the comparison of taxonomic trees.—*Systematic Zoology* 21:390–397.
- . 1986. N-trees as nestings: complexity, similarity, and consensus.—*Journal of Classification* 3:299–317.
- Adams, R. P. 1989. Biogeography and evolution of the junipers of the West Indies. Pp. 167–190 in C. A. Woods, ed., *Biogeography of the West Indies: past, present, and future*. Sandhill Crane Press, Gainesville, Florida, 878 pp.
- Bremer, K. 1992. Ancestral areas: a cladistic reinterpretation of the center of origin concept.—*Systematic Biology* 41:436–445.
- Brooks, D. R. 1990. Parsimony analysis in historical biogeography and coevolution: methodological and theoretical update.—*Systematic Zoology* 39:14–30.
- , & D. A. McLennan. 1991. *Phylogeny, ecology, and behavior*. University of Chicago Press, Chicago, 434 pp.
- Buck, W. R. 1990. Biogeography of the Greater Antillean mosses.—*Tropical Bryology* 2:35–48.
- Burke, K. 1988. Tectonic evolution of the Caribbean.—*Annual Review of Earth Planetary Sciences* 16:201–230.
- Cressey, R. F., B. Collette, & J. Russo. 1983. Copepods and scombrid fishes: a study in host-parasite relationships.—*Fishery Bulletin* 81:227–265.
- Duffield, J. W. 1952. Relationships and species hybridization in the genus *Pinus*.—*Silvae Genetica* 1:93–97.
- Farjon, A. 1996. Biodiversity of *Pinus* (Pinaceae) in Mexico: speciation and palaeo-endemism.—*Botanical Journal of the Linnean Society* 121:365–384.
- , & B. T. Styles. 1997. *Pinus*. Flora Neotropica Monograph. New York Botanical Garden, New York. (in press).
- Fiala, K. L., & R. R. Sokal. 1985. Factors determining the accuracy of cladogram estimation: evaluation using computer simulation.—*Evolution* 39:609–622.
- Gascoyne, M., G. J. Benjamin, & H. P. Schwarz. 1979. Sea-level lowering during the Illinoian glaciation: evidence from a Bahama “blue hole.”—*Science* 205:806–808.
- Govindaraju, D. R. 1984. Mode of colonization and patterns of life history in some North American conifers.—*Oikos* 43:271–276.
- , P. Lewis, & C. Cullis. 1992. Phylogenetic analysis of pines using ribosomal DNA restriction fragment length polymorphisms.—*Plant Systematics and Evolution* 179:141–153.
- Guyer, C., & J. M. Savage. 1986. Cladistic relationships among anoles (*Sauria: Iguanidae*).—*Systematic Zoology* 35:509–531.
- Harmon, M. E. 1984. Survival of trees after low-intensity surface fires in Great Smoky Mountains National Park.—*Ecology* 65:796–802.
- Hedges, S. B., C. A. Hass, & L. R. Maxson. 1994. Reply: towards a biogeography of the Caribbean.—*Cladistics* 10:43–55.
- Klaus, W. 1980. Neue beobachtungen zur morphologie des Zapfens von *Pinus*.—*Plant Systematics and Evolution* 134:137–171.
- Kluge, A. G. 1988. Parsimony in vicariance biogeography: a quantitative method and a Greater Antillean example.—*Systematic Zoology* 37:315–328.
- , & J. S. Farris. 1969. Quantitative phyletics and the evolution of anurans.—*Systematic Zoology* 18:1–32.
- Krupkin, A. B., A. Liston, & S. H. Strauss. 1996. Phylogenetic analysis of the hard pines (*Pinus* subgenus *Pinus*, Pinaceae) from chloroplast DNA restriction site analysis.—*American Journal of Botany* 83:489–498.
- Little, E. L., & W. B. Critchfield. 1969. Subdivisions of the genus *Pinus*. U.S. Department of Agriculture Miscellaneous Publication Number 1144, Washington, D. C., 51 pp.
- McCune, B. 1988. Ecological diversity in North American pines.—*American Journal of Botany* 75:353–368.
- Malusa, J. 1992. Phylogeny and biogeography of the

- pinyon pines (*Pinus* subsect. *Cembroides*).—*Systematic Botany* 17:42–66.
- Mirov, N. T. 1967. The genus *Pinus*. Ronald Press, New York, 602 pp.
- , E. Frank, & E. Zavarin. 1965. Chemical composition of *P. elliottii* var. *elliottii* turpentine and its possible relation to taxonomy of several pine species.—*Phytochemistry* 4:563–568.
- Morrone, J. J., & J. V. Crisci. 1995. Historical biogeography: introduction to methods.—*Annual Review of Ecology and Systematics* 26:373–401.
- Nelson, G., & N. I. Platnick. 1981. Systematics and biogeography; cladistics and vicariance. Columbia University Press, New York, 567 pp.
- , & P. Y. Ladiges. 1991. Three-area statements: standard assumptions for biogeographic analysis.—*Systematic Zoology* 40:470–485.
- Page, R. D. M., & C. Lydeard. 1994. Towards a cladistic biogeography of the Caribbean.—*Cladistics* 10:21–41.
- Perfit, M. R., & E. E. Williams. 1989. Geological constraints and biological retrodictions in the evolution of the Caribbean sea and its islands. Pp. 47–102 in C. A. Woods, ed., *Biogeography of the West Indies: past, present, and future*. Sandhill Crane Press, Gainesville, Florida, 878 pp.
- Pilger, R. 1926. Genus *Pinus*. Pp. 271–342 in A. Engler & K. Prantl, eds., *Die natürlichen Pflanzenfamilien*. Vol. XIII. Gymnospermae, Wilhelm Engelmann, Leipzig.
- Pindell, J., & S. F. Barrett. 1990. Geological evolution of the Caribbean region; a plate-tectonic perspective. Pp. 405–432 in G. Dengo & J. E. Case, eds., *The geology of North America*. Volume H, the Caribbean region. The Geological Society of America Press, Boulder, 528 pp.
- , & J. F. Dewey. 1982. Permo-Triassic reconstruction of western Pangea and the evolution of the gulf of Mexico/Caribbean region.—*Tectonics* 1:179–211.
- Pregill, G. K., & S. L. Olson. 1981. Zoogeography of West Indian vertebrates in relation to Pleistocene climatic cycles.—*Annual Review of Ecology and Systematics* 12:75–98.
- Radford, A. C., H. E. Ahles, & C. R. Bell. 1964. Manual of the vascular flora of the Carolinas. Univ. of North Carolina Press, Chapel Hill, 1183 pp.
- Rohlf, F. J., W. S. Chang, R. R. Sokal, & J. Kim. 1990. Accuracy of estimated phylogenies: effects of tree topology and evolutionary model.—*Evolution* 44:1671–1684.
- Rosen, D. R. 1976. A vicariance model of Caribbean biogeography.—*Systematic Zoology* 24:431–464.
- . 1978. Vicariant patterns and historical explanation in biogeography.—*Systematic Zoology* 27:159–188.
- . 1985. Geological hierarchies and biogeographic congruence in the Caribbean.—*Annals of the Missouri Botanical Garden* 72:636–659.
- Shaw, G. R. 1914. The genus *Pinus*.—*Journal of the Arnold Arboretum* 5:1–96.
- Smith, E. E. 1954. The forests of Cuba. Maria Moors Cabot Foundation Publication No. 2, Cambridge, Mass.
- Smouse, P. E., & L. C. Saylor. 1973. Studies of the *Pinus rigida-serotina* complex. I. A study of geographic variation.—*Annals of the Missouri Botanical Garden* 60:174–191.
- Squillace, A. E. 1966. Geographic variation in slash pine.—*Forest Science Monograph* 10.
- Stevens, P. F. 1996. On phylogenies and data bases—where are the data, or are there any?—*Taxon* 45:95–98.
- Strauss, S. H., & A. H. Doerksen. 1990. Restriction fragment analysis of pine phylogeny.—*Evolution* 44:1081–1096.
- Swofford, D. L. 1991. PAUP-Phylogenetic Analysis Using Parsimony. Version 3.0. Illinois Natural History Survey, Champaign.
- Wheeler, N. C., R. P. Guries, & D. M. O'Malley. 1983. Biosystematics of the genus *Pinus*, subsection *Contortae*.—*Biochemical Systematics and Ecology* 11:333–340.
- Wiley, E. O. 1981. Phylogenetics: the theory and practice of phylogenetic systematics. Wiley, New York, 439 pp.
- . 1988. Vicariance biogeography.—*Annual Review of Ecology and Systematics* 19:513–542.
- Williams, L. 1955. *Pinus caribaea*.—*Ceiba* 4:299–300.

Appendix I

Herbarium specimens from which characters were scored.

Pinus caribaea Morelet var. *bahamensis* Barrett and Golfari. BAHAMAS. Grand Caicos: Correll 49463 (NY). New Providence: Degener 18753 (NY). *P. caribaea* var. *caribaea* Barrett & Golfari. CUBA. Pinar del Rio: Jack 8673 (NY), Leon & Charles 4935 (NY). *P. caribaea* var. *hondurensis* B. & G. BELIZE. Belize: Croat 24005 (MO), Kluge s.n. (MO). Corozal: Crane 315 (MO). Orange Walk: Lundell 677 (MO). Stann Creek: Stevenson 1128 (MO). Toledo: Gentle 3690 (MO). HONDURAS. Gracias a Dios: Clewell 4511 (MO), Nelson & Hernandez 1004 (MO). NICARAGUA. Zelaya: Marshall & Neill 6559 (MO), Seymour 3650 (MO), Stevens 7638 (MO), Stevens 7753 (MO), Stevens 21679 (MO), Vincelli 625 (MO). *P. clausa* (Chapm.) Vasey. USA. Florida: Franklin Co., Godfrey 69282 (LAF); Polk Co., Shuey 2317 (LAF); Walton

Co., Smith 2071 (LAF). *P. cubensis* Griseb. CUBA. Oriente: Ekman 3829 (NY), Shafer 4174 (NY). *P. echinata* Mill. USA. Louisiana: Bienville Par., Thieret 16836 (LAF), Westling 141 (LAF); Evangeline Par., Reese & Reese 1537 (LAF), Thieret 22256 (LAF); St. Helena Par., Allen 1499 (LAF). *P. elliottii* Engelm. var. *densa* Little & Dorman. USA. Florida: Dade Co., Small & Carter 1249 (NY); Monroe Co., Brizicky & Stern 378 (NY). *P. elliottii* var. *elliottii* L. & D. USA. Louisiana: Lafayette Par., Thieret 17423 (LAF); St. Tammany Par., Thieret 16770 (LAF), Thieret 21879 (LAF); Tangipahoa Par., Thieret 16758 (LAF). *P. glabra* Walt. USA. Louisiana: Livingstone Par., Thieret 16743 (LAF); St. Helena Par., Allen 1500 (LAF), St. Tammany Par., Lynch 940 (LAF); Washington Par., Thieret 16782 (LAF). *P. occidentalis* Swartz. DOMINICAN REPUBLIC. Zaroni, Mejia, Pimentel & Garcia 32443 (NY). HAITI. Nash 825 (NY). *P. palustris* Mill. USA. Louisiana: Allen Par., Thieret 10389 (LAF);-Beauregard Par., Thieret 16968 (LAF); Natchitoches Par., Thieret 16811 (LAF), Thieret 17035 (LAF); St. Helena Par., Thieret 17298 (LAF); Tangipahoa Par., Thieret 16782 (LAF); Winn Par., Thieret 16817 (LAF). *P. pungens* Lamb. USA. Pennsylvania: Franklin Co., Adams s.n. (LAF), Adams 25 (LAF). *P. rigida* Mill. CANADA. Quebec: Lemieux 1281 (LAF). USA. Maryland: Frederick Co., Windler & Stastny 3900 (LAF). North Carolina: Buncombe Co., Dunton s.n. (LAF); Jackson Co., Duncan 22793 (LAF). Pennsylvania: Franklin Co., Adams s.n. (LAF). West Virginia: Hardy Co., Wratchford s.n. (LAF). *P. serotina* Michx. USA. Alabama: Geneva Co., Kral 33947 (LAF). Georgia: McIntosh Co., Duncan 20688 (LAF). South Carolina: Charleston Co., Ahles 53156 (LAF), *P. taeda* L. USA. Louisiana: Livingston Par., Thieret 16742 (LAF) Thieret 16753 (LAF), Thieret 16754 (LAF); St. Helena Par., Thieret 17300 (LAF); Tangipahoa Par., Thieret 16756 (LAF). *P. virginiana* Mill. USA. Alabama: DeKalb Co., Vincent 1281 (LAF). Georgia: Rabun Co., Reade s.n. (LAF). Maryland: Allegany Co., Duncan 22944 (LAF). North Carolina: Orange Co., Ahles 53117 (LAF). Tennessee: Cheatham Co., Demaree 49183 (LAF).

Appendix II

Twenty-one morphological characters used in this study. The first fourteen characters describe mature

megasporangiate cone morphology and the last seven describe needle morphology.

- (1) Sum of maximum cone length and maximum cone width: less than 20 cm = 0; greater than 20 cm = 1.
- (2) Cones sessile or stalked = 0; sessile = 1.
- (3) Transverse keel or dorsal surface of cone scale between apophysis and umbo: depressed at junction = 0; continuous at junction = 1.
- (4) Lateral portion of most umbos not strongly elevated above apophysis = 0; strongly elevated above apophysis = 1.
- (5) Umbo: weakly keeled or unkeeled = 0; strongly keeled = 1.
- (6) Umbo keel: straight or monotypically curved = 0; undulating = 1.
- (7) Proximal portion of umbo slopes at: high angle or is perpendicular to apophysis surface = 0; low angle from spine to proximal edge of umbo = 1.
- (8) Proximal portion of umbo: not concave = 0; concave = 1.
- (9) Portion of umbo proximal to keel: not larger than distal portion = 0; much larger than distal portion = 1.
- (10) Junction of distal margin of umbo and apophysis: grooved = 0; not grooved = 1.
- (11) Spine on umbo: unkeeled on apical half = 1; keeled on part of apical half but unkeeled at apex = 2; keeled on all of apical half = 3.
- (12) Spine on umbo: reflexed = 0; straight or curved outward = 1.
- (13) Spine: connected to keel = 0; substantially distal to keel = 1.
- (14) Most umbos erect such that apex of spine is not pointed distally near the level of the apophyseal keel = 0; most umbos flattened and turned distally such that apex of spine is pointed distally near the level of the apophyseal keel = 1.
- (15) Needle number: 2 = 1; 2(-3) = 2; 3(-2) = 3; 3 = 4; 3(-4) = 5; 3-5 = 6.
- (16) Hypodermal cells in leaf angles: absent = 0; present = 1.
- (17) Hypodermis structure: uniform = 0; biform = 1.
- (18) Endodermal cells: walls normal = 0; walls thickened = 1.
- (19) Resin canals medial = 0; internal = 1.
- (20) Number of resin canals: coded character.
- (21) Number of stomata: coded character.